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LXVIII.—*A suggested Origin of the Segmented Worms, and the Problem of Metamerism.* By H. M. BERNARD, M.A. Cantab.

DURING the last five years in which I have been working at the stony corals, the Cœlenterata, as an animal group, have been more or less continuously in the foreground of my imagination. I do not pretend to have seriously worked at any other than the Madreporaria; yet the fact just stated will, I trust, be accepted as some excuse for the following article. In it I propose to show how the Cœlenterates may have given rise to the segmented Worms. The idea forced itself upon me by its simplicity, and, although not altogether new, it has never, so far as I am aware, been stated as here proposed. I may add that I am still further impelled to trespass beyond the region of my own serious studies by perceiving that, if there is any truth in the suggestion, it offers a possible solution to that vexed problem "What was the origin of the mesoderm?"

In the geological record metamerism first appears in the Trilobites, which are constructed of a number of segments jointed together. With the exception of a head-piece and, in most cases, a tail-piece, which differ from one another and

from the other joints, all the segments in the typical Trilobite are alike in form; they diminish in size, however, progressively from front to back. Further, with regard to the head-piece, it is not difficult to see that this has been built up of a certain number of fused and thus modified segments. The same is true of the tail-piece, as we gather not only from its markings but also from the fact that some of the very oldest Trilobites are found without any such specialized fusion of segments. Characteristic of the Trilobite segment is the pair of immense pleural folds, which can only be regarded as secondary specializations. We conclude, then, that the Trilobites must have been descended from some form made up of simpler segments, *i. e.* of segments without pleuræ, and that these segments, with the exception of the first, containing the mouth, and the last, containing the anus, were in all respects similar in form, but *diminished progressively from the oral to the anal end*.

We look elsewhere, then, for more primitive segmentation than that which we find in these ancient fossils. We have not far to look, for there exists a group in which it attains its greatest development, the primitive segments being apparently but little altered by secondary specializations. I refer to the segmented Worms. In typical forms we have here a long string of segments, the first and the last alone being peculiar; all the rest, no matter how many, are structurally exact repetitions of one another. Not only are the appendages and markings of the segments faithfully repeated from segment to segment, but if cut open the internal machinery of each segment, excluding the reproductive, is found simply to repeat the internal machinery of that which precedes it; muscles, nerves, blood-vessels, excretory organs, are all more or less exactly repeated.

That metamerism reaches its highest development in the Worms there can then be no doubt; hence it is to animals below the Worms in structural complexity that we must look for its origin. Where segmentation or vestiges of it are found in animals above the Worms—for instance, we have traces of it in ourselves—we are justified, in the absence of clear evidence to the contrary, in assuming that it has been derived from Annelidan ancestors. It is to my mind almost outside the bounds of probability that such a remarkable repetition of parts could have been developed twice on quite independent lines.

Now the problem is, How did such an animal come into being? Several interesting suggestions have been made,

but zoologists have not been able to agree as to the process which best satisfies the conditions. But, on the other hand, zoologists are all, I think, agreed that the form which comes with the greatest probability next below the typical segmented Worm is the Cœlenterate; for as yet no satisfactory position has been found for the other groups of vermiform animals, and though we usually place them near one another, we travel outwards from the typical Annelid towards these groups with uncertain steps. We only reach solid ground again when we come to the Cœlenterates. Morphologists have, indeed, long recognized that the Cœlenterate body marks a well-defined stage in the evolution of the Metazoa. The mechanism is simple, yet very perfect, for the two primary functions of animal life, the vegetative and the reproductive. Its success may be gathered from the extraordinary wealth of the Cœlenterates still peopling the waters of our planet both in numbers and in forms. But we are justified in assuming that this success has attended them from their first appearance in early geological periods, bearing in mind that, as we go back to simpler conditions of environment—simpler in the fact that many animal forms preying and to be preyed upon were not then evolved,—the variations in form would be less and less numerous, until we reach a time when the simplest of all conceivable types of Cœlenterate was the only representative of the race.

It is to the Cœlenterates therefore that we naturally look first for the ancestors of the segmented Worms, and more than one attempt has been made to sketch the form-changes which would be necessary. So far as I remember, the earliest and, to my mind, the best suggestion refers the segmented Worms to the serial budding which is known to occur among the Cœlenterates, *e. g.* in the "strobila." This is, however, so far only a suggestion; I know of no attempt to work it out in detail; one apparently insuperable difficulty blocks the way, *viz.* the presence, in the Annelids, of the cœlomic cavities, which are unknown in the Cœlenterates. Prof. Sedgwick* proposes to deduce the cœlomic cavities of the Annelids from the mesenterial chambers ("gastric pouches") of a Cœlenterate-like ancestor. This would not explain the addition of new segments, progressively diminishing in size, at the posterior end. The method of the increase in the number of the mesenteries which takes place in the higher Cœlenterates is quite different. It seems to me that the reference of

* Quart. Journ. Micr. Sci. xxiv. (1884).

segmentation to serial budding is singularly apt. No group of animals before or since, excluding perhaps the Protozoa, have shown such marvellous developments of this method of reproduction. The number of successful colony-formations among the Cœlenterates, both stationary and free-swimming, is perfectly bewildering. We have, then, in this power of increase by budding a wealth of possibilities upon which we can safely draw without putting any strain whatever upon our sense of what is probable. I go even further, and think it possible to show that free-swimming strings of buds must at one time have existed as a necessary interaction between an organism like the Cœlenterate, capable of budding anywhere, and its environment.

I prefer, then, to go lower down among the Cœlenterates than Prof. Sedgwick, lower down either phylogenetically or ontogenetically, for the origin of the Annelids—*i. e.* to forms either primitive or larval, and before the mesenteries (which, I think, developed as muscular bands drawing and holding in the primitive mouth in order to form an œsophageal infolding*) appeared.

The chief assumption which we have to make, then, is that some free-swimming ciliated Cœlenterate of the very simplest type, instead of becoming early attached, continued to be free-swimming long enough to put out buds. There is nothing improbable in this. Drifted away by currents, thousands must have missed finding anything to attach themselves to. In times before the seas swarmed with carnivorous fish or Crustacea—both, I believe, descendants of the Worms whose origin we are discussing—there would be abundance of opportunity for some of these unattached forms to lead a free-swimming life with safety, feeding on still simpler forms, animal and vegetable.

* This method of deducing the Scyphozoa with ectodermal gullet from the Hydrozoa without ectodermal gullet is to my mind preferable to the belief, entertained by Sedgwick and others, that the mesenteries were developed primarily as folds for the increase of the digestive surface. The differentiation of the muscles round the primitive mouth into radiating bundles could hardly fail to result in the formation of internally projecting folds, the body being but a flexible sac frequently distended by fluid. The more strongly these ridges developed the more permanent would be the tucking of the primitive oral aperture into the body, the ectoderm around it becoming the lining of an œsophageal tube. The advantages to the organism not only of this more perfect mouth, with its stronger sphincter and radial muscles, but also of the increase in the digestive surface afforded by the mesenterial folds, would lead to its further development.

We merely assume, then, that a certain number of forms remained free-swimming long enough to feed and to grow and to put out buds. Now, without going so far as to say that there is only one place where such a free-swimming form *could* bud and yet continue to pursue its active life, viz. at its hinder end, it is certainly clear that the most likely place for a bud to appear would be at the posterior end. Not only would any other place make forward locomotion impossible, but at the hinder end the conditions seem to be more favourable than anywhere else. The external pressure would here, in the wake of the animal, be less than anywhere else in the body—indeed, during rapid forward swimming there would be something like suction at this spot. Now if this is true for the first bud, it is surely more true for the second, and it seems clear that we get all the conditions for rapid serial budding: for the addition of the first bud, by increasing the number of available cilia, would propel the animal faster through the water; this greater speed would enable more food to be swallowed, part of which would find its way into the bud, while at the same time it would still further diminish the external pressure of the water at the extreme hinder end, and we have still more favourable conditions for the formation of a second bud behind that already formed, and so on. If there is any probability in this argument at all, it would seem that the more buds there were the faster would buds be produced, until some limit, presently to be discovered, was reached.

But apart from this argument, and merely bearing in mind the wealth of colony formation developed among the Cœlenterates, is there not full justification for believing that round the shores of the ancient seas, soon after the primitive forms appeared, there would be free-swimming individuals trailing behind them longer or shorter strings of buds diminishing in size progressively backwards? Of these, some, we may fairly assume, would sooner or later again give up more or less completely the laborious free-swimming life and become creeping forms. It is in this direction that I should be inclined to look for the ancestors of some of the other members of the ancient class "Vermes" *.

* The Turbellarian *Microstomum lineare*, Ehr., still swims about trailing short strings of buds after it. I was once fortunate enough to get a glimpse of it living, under a high power, and saw very clearly what appeared to be typical nematocysts scattered here and there in its skin. The derivation of the Plathelminthes from primitive Cœlenterates, which gave up a free-swimming for a creeping manner of life, has much to be

But confining our attention solely to the forms which we assume persisted in their more active free-swimming habits, a vista of possibilities opens out with regard to them which seems to lead straight to the typical Annelid.

It appears at first sight as if there would be no limit to the possible addition of fresh buds, so that, excluding accidents, each original (or parent) animal would soon trail after it a string of buds of indefinite length. Mechanical difficulties, however, would most certainly sooner or later arise. The most important difficulty would, it seems to me, be the following:—The first-formed buds would have considerable difficulty in getting rid of the indigestible remains of their food. The parent animal, or first segment, was probably able to get rid of faecal remains through the mouth; but this would be very difficult for the buds, and, indeed, progressively difficult the further back they were. The aperture leading from sac to sac we may justly presume to have been, at least primitively, very small, and it may perhaps have remained so in the immediate ancestors of the segmented Worms. Before long, therefore, particles of faecal matter would be mixed with the food which found its way back into the last-formed bud, until in time the faecal matter from the progressively increasing number of digesting buds would make the arrival of food-particles from the mouth impossible. Some nutriment might for a while be extracted from this faecal matter, but the posterior segments would eventually be so poorly nourished that further budding would cease. This difficulty was hardly likely to last long. Apertures can occur almost anywhere in the Cœlenterate wall, as we know from the apertures in the walls of the Sea-anemones for the discharge of acontia. Hence a posterior opening might early be developed in order to free the terminal buds from their useless and deleterious burden *. The muscular fibres of the walls would provide the

said for it. The tentacles of *Temnocephala* may be secondary adaptations to its sessile manner of life; but the fact discovered by Professor Haswell (Quart. Journ. Micr. Sci. xxviii., 1888), that the young of the Australian forms invariably have six, while the adult has only five tentacles, is significant rather of the opposite view. My esteemed friend and teacher Prof. Arnold Lang (Text-book of Comp. Anat. pt. i.) also suggests an origin from free-swimming Cœlenterates which have secondarily adopted a creeping manner of life, but along an entirely different line, viz. through the Ctenophora, certain specialized forms of which furnishing almost ideal intermediates.

* (Cf. Prof. Sedgwick's account (*l. c.*) of the possible origin of nephridial apertures out of the constricted gastric pouches, which, according to his theory, gave rise to the coelomic chambers.

sphincters. Such an anal aperture, acquired of necessity by the lengthening chain of digesting buds, would be earlier and earlier developed by that force in living matter called heredity, which causes it to repeat itself so long as the habits of life demand.

This specialized aperture, however, would now be in the exact position from which budding had formerly taken place. Although division of highly organized cells is known in the Protozoa, it is certainly commoner in cells not differentiated for special functions. Hence we may suppose that the cells which were specialized as epithelial, muscle-, or nerve-cells to line and regulate the new opening would not divide, at least actively, but the less differentiated zone of cells immediately round these would, and by so doing push the specialized anus out in front of them, so that it would always be at the posterior end of the chain.

At first this anal aperture would have been very simple and small, but as it became more highly specialized the budding zone would retreat from the extreme tip until there appeared a regular "anal segment," the budding zone being always between it and the last-formed bud. This is, in fact, still the law in all animals that develop metamerically—the new segments are added between the anal "segment" and the one in front of it.

The mechanical difficulty due to the accumulation of faeces being thus simply got over, the possibility of further advance is instantly furnished; more food would now be passed along, and the posterior segments being better nourished, the budding process at the end could be renewed. The number of buds would, however, still be limited, as, even though faecal matter could now be got rid of, yet as the length increased it is obvious that more faecal matter than food would reach the posterior end of the body, which would thus be badly nourished and cease to grow. This limit could only again be surmounted by the development of a vascular system.

So far, then, we have arrived at long free-swimming strings of Coelenterate buds with a mouth at one end and an anus at the other, and with a tendency to produce fresh buds up to a limit between an anal prominence or segment and the last-formed bud. This brings us so near to the typical Annelids that it is worth seeing whether the structural differences which still separate them are insurmountable. Here I might parenthetically remark that it is just such active free-swimming organisms as those we have sketched which attain to higher levels of organization. They, least of all, would

stand still in the midst of the developing life of the sea. We have a right to expect that, if in the age of the Cœlenterates any such forms existed, profound structural modifications for the perfecting of their activities would take place in them.

The difficulty, and the only great difficulty, which lies in the way of the deduction of the typical Annelid from the hypothetical organism described above, lies in the fact, already mentioned, that the former have paired cœlomic cavities. The rise of these in the animal kingdom is still one of the great riddles of zoology. Professor Sedgwick's suggested solution, which has been deservedly widely accepted, would, I think, have satisfied me entirely had division of existing segments been the rule for their multiplication. As it is, their known method of production has always seemed to me to point so unmistakably to serial budding, that nothing which has been said on the subject has been able to deter me from watching for clues in that direction. On the other hand, his argument based upon the blastopore is very complete, and, so far as I can see, can only be attacked as coming too much within the field of purely developmental adaptations. I repeat, then, that this paper will have some value if it suggest a simple and natural line of development for these cavities—that is, a line of development without resort to any hypothetical "change of function," which is one of the convenient stocks-in-trade of the puzzled morphologist;—if it show that in the further development of strings of Cœlenterate buds as free-swimming organisms some such mesodermal structures would inevitably arise, fulfilling essentially the same function from their earliest rudiments to their latest specialization.

We are safe in assuming that the body-cavities arose, as all new structures arise in the animal kingdom, in response to some physiological need. In the present instance we do not require to look far for that need. In the struggle for existence between such chains of Cœlenterates it is not likely that the muscles in the walls would be long kept out from assisting in locomotion. A waving of the body is a far more efficient method of propulsion than the rowing of cilia. Hence we should expect the wall-muscles in each bud to be gradually specialized into systems in order to bring about definite serpentine movements of the whole string, and, increasing in size and strength, gradually to take on the whole function of propulsion. But muscles require not only to be fed and oxygenated, but also to be relieved of the waste products of their activities. The more they are used the more elaborate must be the nutritive and excretory apparatus to enable them

to maintain their efficiency. Further, this growth and ever increasing concentration of the muscular systems of the individual buds would necessarily be accompanied by an ever increasing development of their nervous systems. These also would require to be well nourished and cleansed. The feeding and the carrying away of the waste products of this developing neuro-muscular sheath could hardly be carried on in the original Cœlenterate wall. Structural modifications, increasing in specialization as the systems they subserved became more and more perfect, were bound to take place; these, I think, we may safely outline. In the simpler stages scattered cells with fluid spaces would appear in the mesenchymal layer; their increase would result in the development of a parenchymatous tissue, with still larger fluid spaces, for a compact tissue would be a hindrance to contractility. These spaces would gradually separate the ectoderm from the endoderm—*i. e.*, on the one hand, the ectodermal layer and locomotory muscles from the digesting endoderm, the only source of nourishment; and, on the other hand, the digesting endoderm from the ectoderm, the only breathing surface. Further advance along these lines would necessitate definite streams, and ultimately a vascular system, collecting nutriment from the digesting layer and oxygen from the ectodermal. In this way, then, the endoderm and the ectoderm would be gradually divorced from each other by an increasing development of intervening tissue. The former (endoderm) would be ultimately confined to a central hollow strand, the alimentary canal, suspended and held in place by membranous tissue and wrapped round by muscles and cells split off from the early mesenchymatous or parenchymatous layer already described. In passing we may note that though the deep columnar epithelium characteristic of the alimentary canal of the Annelids could doubtless be developed at any time, still it is just possible that it may be an expression of the shrinkage of the surface due to the detachment of the endoderm from the outer wall and to its becoming the inner lining of a narrowing axial tube. The suggestion arises naturally from the remarkable difference seen between the endoderm of an expanded and that of a contracted polyp.

Here, then, we have a very simple and natural origin for the mesoderm in the Metazoa, the activities of our string of buds supplying us with an adequate reason for its development. The case is, I think, a strong one, for the muscles in each bud necessary to enable it to take its share in giving to the whole string a serpentine movement would have to be

far stronger than any which the bud itself would require had it existed as a single animal. Similarly the nervous system necessary to coordinate the movements of these muscles within each bud and with those of the buds before and behind it would have to be very much more highly developed than would have been necessary in single animals the size of the buds or segments. We need not be surprised, then, at the enormous development of the mesodermal chambers. It is significant here to note that the Turbellarians, which I am inclined to regard as the nearest existing kindred of our early strings of buds, having, with a few exceptions, lost the power of forming buds, have their muscles and nerves simply embedded in a parenchymatous tissue not unlike that which we imagine to have been a stage in the development of the mesodermal cavities of the Annelids. Neither muscles nor nerves in these single animals required the same high specialization as was required by the individuals forming the separate links in a long chain which had to move as one, comparatively speaking, immense composite organism. We thus have, in the specially pronounced development of the neuro-muscular sheath of each segment of our string of buds—a far more developed sheath, I repeat, than any single animal could possibly require,—an efficient cause to account for so highly specialized a nutritive and excretory apparatus as the mesoderm of the Annelids, with its cavities, vascular system, and nephridial funnels.

On turning to the embryological records of the mesoderm we find them confused, and, for want of a clue, frequently contradictory. We have the coelomic cavities arising in masses of parenchymatous tissue, or forming early out of very few cells, or, again, as definite invaginations. All these fall into their places in the light of the origin above assigned to the mesoderm. They are fragments and abbreviations of the true phylogenetic history. The invaginations may be either for the purpose of rapidly supplying cells or else as shortened methods of forming the coelomic cavities. They obviously serve both purposes.

We have here an excellent illustration of the difficulty of discovering phylogeny from embryology. The parenchymatous mesoderm suggests little or nothing, whereas mesodermal invaginations seem so clearly to indicate some once useful structures which, by "change of function," might have supplied the mesoderm, that they immediately acquire a greater importance than really belongs to them. One primitive function to which they have been attributed—besides

that suggested by Professor Sedgwick, that they were at one time due to foldings of the digestive layer—is the reproductive. But I cannot help remarking that the view here put forward, which regards the mesoderm as arising by gradual structural modifications in response to the simplest and most frequently recurring of life's activities, viz. to locomotion in pursuit of food—that is, to locomotion which lasts from the beginning to the end of life,—supplies us with a better motive for its production than do the needs of the reproductive function, which are periodic and confined to the adult. Further, I need hardly again emphasize the fact that the suggested origin put forward in this paper avoids all appeals to "change of function"; from its earliest rudiments to the highest specialization the mesoderm, if developed along the lines here sketched, had essentially the same function.

With the perfection of the powerful neuro-muscular sheath and the necessary mesodermal apparatus for its nutrition and excretion we have brought our strings of Coelenterate buds near enough to the typical Annelid to show that, whether this was the true origin of the Annelids or not, it could easily have been so. It is admittedly only an outline sketch. A much closer comparative study of kindred animals and of their homologous structures would be necessary in order to fill in details. One somewhat prominent point may, however, be noted.

For the purpose of bringing about the strong lateral contractions of each segment necessary to give the whole complex its serpentine motion, the longitudinal muscles would tend to stretch from end to end of each segment. Their points of insertion would consequently be more and more concentrated at the ends of the buds, leaving the middle regions free. As already noted, the ectoderm was the only available respiratory surface. What more natural than that this middle region should become specialized for respiration, the greatly developed neuro-muscular system demanding for its efficiency ever-increasing supplies of oxygen. The necessary mechanism for obtaining this extra supply was well within reach and the structures developed would be from the first functional. I refer to the lateral skin-folds which would arise in the middle regions above mentioned every time the longitudinal muscles contracted. From this point of view the parapodia, whatever specialization and differentiation they may since have undergone, were originally nothing more than gill-folds, and they arose concomitantly with the rise and concentration of the powerful longitudinal muscles as these latter required more and more oxygen for their work.

We can thus trace our rows of Coelenterate buds along a line of development, each step in which, so far as I can see, would be a necessary result of their locomotory activities, not as so many separate buds, but acting together as a single complex organism. This line has led us, without strain or difficulty, to the typical Annelid with its coelomic cavities and its parapodia.

On page 2 I stated that I considered the metameric segmentation so remarkable a phenomenon that wherever traces of it can be discovered we are justified in assuming descent from Annelidan ancestors. The segmentation found so widely spread in the vegetable kingdom is a parallel phenomenon, being due to periodical buddings. In the Vertebrata we have organisms which show very distinct traces of segmentation, but complicated by the fact that their most characteristic structure, the notochord, shows no traces of having been primitively segmented. The jointing which later appears in the vertebral column has apparently been impressed upon it as a mechanical necessity by the segmented organism in which it developed. For an attempt to show how the vertebrate organization with its primitively unsegmented notochord can be deduced along what appears to be a similarly straightforward line of mechanical adaptations from an annulate ancestor, see "A new Reading in the Annulate Ancestry of the Vertebrata," *Natural Science*, vol. xiii. 1898, p. 17.

[NOTE.—This paper was written eighteen months ago, and was finally corrected for press before the appearance of Prof. Lankester's critical *résumé* of the subject in the recent instalment of his 'Text-book of Zoology.']

LXIX.—*On some little-known African Silurid Fishes of the Subfamily Doradinæ.* By G. A. BOULENGER, F.R.S.

AMONG the least-known freshwater fishes of Africa there is a group of small or very small Silurids, more or less closely allied to *Synodontis* and falling under Günther's division "*Stenobranchiæ*," which have been described in a more or less satisfactory manner by various authors under the generic names of *Mochocus*, *Rhinoglanis*, *Chiloglanis*, *Doumea*, *Atopochilus*, and *Peltura*. Having lately had the privilege of examining the few specimens of these fishes preserved in the